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THE UNIVERSITY OF ALBERTA

The Influence of Environmental Factors and Piscivory in Structuring Fish Assemblages of Small Alberta Lakes

by

© Clifford L. K. Robinson

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Zoology

EDMONTON, ALBERTA

Spring, 1988

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ISBN 0-315-42880-5

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THE UNIVERSITY OF ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE INFLUENCE OF ENVIRONMENTAL FACTORS AND PISCIVORY IN STRUCTURING FISH ASSEMBLAGES OF SMALL ALBERTA LAKES SUBMITTED BY Clifford L. K. Robinson in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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ABSTRACT

Forty-five small lakes were surveyed in central Alberta, from May-August 1986 and 1987, to determine if discrete, repeatable fish assemblages exist and to identify the main environmental and biotic processes likely responsible for any assemblage-level patterns. Overall, 11 species of fish were caught in 36 lakes; nine lakes were fishless. Hierarchical classification and detrended correspondence analysis of fish species presence/absence identified two main assemblage types characterized by northern pike (Esox lucius) /yellow perch (Perca flavescens) and brook stickleback (Culaea inconstans)/fathead minnow (Pimephales promelas). Environmentally, pike/perch lakes were significantly deeper and larger in surface area than lakes of the stickleback /fathead assemblage type. Piscivory appears to be the dominant process in maintaining nearly complete negative associations between members of the two assemblage types. The importance of piscivory was further supported by examining, in the laboratory, the survival rates of all possible combinations of brook stickleback, fathead minnow, finescale dace (Phoxinus neogaeus), and yellow perch in the presence of northern pike. Overall, results of this study are comparable to those from environmentally different and species rich regions of southern Ontario and northern Wisconsin. For small lakes, piscivory and few abiotic factors (maximum depth, surface area, and isolation), appear most important in structuring fish assemblages.

Acknowledgements

This research was generously funded by grants from the Boreal Institute for Northern Studies to myself and to my supervisor Dr. W.M. Tonn and by a Natural Sciences and Engineering Research Council of Canada operating grant to Dr. W.M. Tonn. Logistic support and facilities provided by Dr. E.E. Prepas at the Meanook Biological Research Station, Dr. W.C. MacKay at the Lac St. Anne field station, and Mr. C. Rentz at the Canadian Forestry Service field camp near Hinton were very much appreciated. Many thanks are due to the students, staff, and researchers associated with the MBRS, for their help and encouragement with my research. I particularly wish to thank Mark Olson for making the field work an enjoyable experience, Lorne LeClair and Rob Appleton for logistical assistance, Gurtie Hutchinson for water chemistry analysis, and Dr. Pat Chambers, Jackie Shaw, and Wayne Roberts for "research" discussions. Finally, I greatly appreciated the support provided by my supervisor Dr. W.M. Tonn, and discussions with and critical thesis reviews by Drs. W.M. Tonn, J.S. Nelson, M. Dale, and C.A. Paszkowski.

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1. FACTORS STRUCTURING FISH ASSEMBLAGES: AN OVERVIEW

1.1 INTRODUCTION

Glaciated regions of North America presently contain a large number of small lakes that are potentially available for fish to inhabit. Results of community studies from north-central districts of the continent (Harvey 1978, 1981; Tonn and Magnuson 1982; Rahel 1984; Eadie and Keast 1984), suggest that these lakes do not contain random mixtures of fish species that are influenced merely by chance or regional-historical events but rather a small number of repeatable species assemblages that are influenced by:

1. factors related to colonization (e.g., lake isolation).

2. factors related to either maintenance of a species population after it has colonized a lake, or to the population's local extinction following colonization (e.g., lake size, habitat diversity, habitat severity).

3. biotic interactions (e.g., competition, predation).

1.2 COLONIZATION EVENTS

Colonization by fish of lakes within a new boreal watershed may be considered analogous to species colonization of oceanic islands (Magnuson 1976). Geographical ecologists have identified several characteristics of islands that influence the number and kinds of species that can colonize them (MacArthur and Wilson 1967). A number of these characteristics have been examined relative to post-glacial dispersal (Crossman and McAllister 1986) and subsequent development of fish assemblages in boreal lakes (Stewart and Lindsey 1983).

The theory of island biogeography, suggests that lakes more isolated from a source of species (e.g., a large lake or river) will have lower assemblage diversity than lakes closer to a source. After moving into a new watershed, a species' dispersal may be limited by physical barriers (e.g., waterfalls) and/or the filtering nature and potential seasonal instability of connecting waterways (Barbour and Brown 1974; Browne 1981).

Various measures of lake isolation (e.g., presence or absence of an outlet, size of the outlet's watershed, distance and gradient from a source of colonists) are significantly related to fish assemblage richness and composition (Tonn and Magnuson 1982; Rahel 1984).

Dispersal mechanisms used by fishes to enter isolated lakes may include the ability to move through small and temporary quantities of surface run-off, wind transport (Bajkov 1949), underground streams (Nelson and Paetz 1974), past connections, and man (Rahel 1984). The first three dispersal mechanisms support the observation that most isolated lakes contain small bodied fish species (e.g., minnows and sticklebacks). Man represents an important and often overlooked selective dispersal factor (e.g., Magnuson 1976).

Another "colonization" variable that contributes to the relatively depauperate diversity in northern lakes is the age of these systems (Barbour and Brown 1974). Northern watersheds in glaciated regions are generally too young to have evolved endemic species or to have allowed all potential species the chance to reach otherwise suitable habitats (Magnuson 1976). However, the history of each region must be considered before broad generalizations are appropriate.

1.3 EXTINCTION EVENTS

As colonization of boreal lakes proceeds, events related to local extinction of fish species within a lake influence assemblage structure. Three important extinction-related variables discussed in the literature are lake size (and/or habitat heterogeneity), habitat severity, and biotic factors

(predation and competition). Ultimately, one expects an interaction between colonization and extinction such that an equilibrium number of species is maintained (MacArthur and Wilson 1967; Magnuson 1976).

1.3.1 Lake size and habitat heterogeneity

Larger lakes should contain a greater variety of habitats than smaller lakes. Therefore, larger lakes should have an increased number of sites for reproduction, a greater diversity of vegetation for cover, etc., and thus should be able to support more fish species. Eadie and Keast (1984) found that in boreal lakes of Ontario fish species diversity was significantly and positively related to both surface area and several measures of habitat complexity (plant species diversity, substrate diversity). Similarly, Tonn and Magnuson (1982) determined that species richness in Wisconsin lakes was correlated with lake area and vegetation diversity, which in turn, were correlated with each other. It has not been established that species richness in boreal lakes is related to area independent of habitat diversity, as predicted (MacArthur and Wilson 1967) and found elsewhere (Simberloff 1976).

1.3.2 Environmental severity

Studies of adaptations of fishes to chemical conditions of small boreal lakes have focussed on responses to low pH and low dissolved oxygen concentrations, two common features

of these ecosystems. These studies have found that the distribution and abundance of species among lakes with different chemical conditions are related to physiological tolerances.

Several studies have shown that pH is one of the most important environmental characteristics distinguishing boreal lakes that contain different types of fish assemblages. This is especially true in continental shield regions, where many poorly-buffered lakes have pH values near or below tolerance levels (Rahel 1984). Because of the strong correlation between species richness and pH, Henderson (1984) suggested that fish assemblages of acidic waters are not unique combinations of species but rather are simply reduced forms of assemblages found at higher pH levels. The close correspondence among rankings of species occurrence with mininum pH in naturally acidic lakes (northern Wisconsin), occurrence in lakes affected by acid precipitation (Ontario), and rankings based on survival during laboratory exposure to low pH, support Henderson's conclusion that low pH is directly responsible for reductions in species richness and composition (see also Rahel and Magnuson 1983).

Another factor complicating an evaluation of the effects of pH is the fact that many other environmental characteristics covary with pH. Boreal lakes with naturally low pH tend to be small, isolated, and have low alkalinities and limited habitat diversity, all of which may reduce species richness in a selective manner. Indeed, Rahel (1986)

observed that low-alkalinity lakes (pH > 5.0) had fewer species than high-alkalinity lakes and added species at a slower rate as lake size increased. Rahel (1984) also concluded that a sequential loss of fish species occurs in isolated dystrophic lakes as bog mat development decreases lake size and eliminates the littoral zone, as well as acidifying the water. Still, Rago and Wiener (1986), using analysis of covariance and a blocked comparison test to remove effects of lake area, found that Ontario and Wisconsin lakes with low pH (< 6.0) contained significantly fewer species than lakes with pH > 6.0.

From these studies it appears that: (1) naturally low pH, common to many boreal lakes, can prevent establishment and maintenance of fish populations due primarily to reduced reproduction and increased mortality of eggs and larvae (e.g. Rask 1984a, b), and (2) environmental covariates of low pH also effect fish species richness and composition. Thus, although pH is not the only factor influencing the structure of fish assemblages, it is usually an excellent empirical predictor of species richness and presence or absence of individual species.

Another chemical condition that is thought to be important in structuring fish assemblages is the extreme depletion of dissolved oxygen which occurs frequently in small boreal lakes during winter. Because of the high sediment surface:water volume ratio of shallow lakes, the amount of dissolved oxygen consumed by processes of

decomposition can approach the total amount of oxygen dissolved in the water. During the long boreal winter, a continuous cover of ice and snow can severely reduce the amount of light entering a lake, preventing the generation of fresh oxygen from photosynthesis. As the ice thickens from the surface downward, an anaerobic layer develops along the bottom and expands upwards (Magnuson and Karlan 1970). As living space decreases, the lake may experience a fish kill. Behavioral adaptations of some fishes in response to increasing anoxia may include redistribution to aerobic refuges within the lake or emigration from the lake (Magnuson et al. 1985). Physiological adaptations associated with small body size and "air-breathing" may also allow certain fishes to survive winter hypoxia (Casselman and Harvey 1975; Klinger et al. 1982; Magnuson et al. 1983). As a result, winterkill is a selective mortality factor that can alter the composition of fish assemblages in small boreal lakes.

Tonn and Magnuson (1982) were able to separate fish assemblage types in northern Wisconsin lakes based on a combination of winter oxygen concentration and lake isolation. In more isolated lakes experiencing hypoxia, assemblages dominated by central mudminnows (Umbra limi) and minnows (Cyprinidae) occurred whereas in lakes with outlets, or in deeper lakes having sufficient oxygen supplies, assemblages were characterized by northern pike (Esox lucius), largemouth bass (Micropterus salmoides), and other centrarchids. Tonn and Magnuson concluded that mudminnows and

cyprinids could persist in shallow isolated lakes because of physiological and behavioral adaptations allowing survival under low oxygen conditions. These physically harsh habitats in turn offered refuges from piscivorous predators. A different refuge was available to pike; as winter conditions proceeded they apparently emigrated from the lakes and survived in outlet stream refugia, returning to the lake in the spring. By exploiting this refuge, pike were able to avoid the harsh abiotic lake environment and exclude the predation-intolerant mudminnow and cyprinids.

1.3.3 Lake Productivity

Relations between species composition and some correlate of lake productivity (alkalinity, phosphorus concentration, total dissolved solids, etc.) have been useful predictors of boreal fish assemblages. Theoretically, more productive habitats should maintain more fish species as a result of increases in planktonic and benthic prey abundance/diversity. For example, Gascon and Leggett (1977) found that diversity of the littoral fish community within Lake Memphremagog (Quebec-Vermont) was positively correlated with a nutrient production gradient.

Correlations between prey abundance/diversity and fish species diversity may be a result of fish and prey responding independently to physical environmental parameters. Harvey (1975) found a strong correlation between the number of zooplankton species and fish species in a group of Ontario

lakes, but concluded that this correlation was due to independent correlations with physical/chemical features of the environment rather than cascading actions between trophic levels.

Differences in assemblage diversity between lakes of northern and southern Ontario also support the diversity/productivity theory. Less productive lakes in northern Ontario tend to have lower vegetation and invertebrate prey abundance/diversity than southern lakes and a corresponding reduction in fish species number (Eadie and Keast 1984). However, as with pH, assigning cause-and-effect in productivity/fish assemblage relations is difficult, because several alternative factors, e.g., habitat diversity, covary with productivity gradients.

1.4 BIOTIC INTERACTIONS

Prediction of fish assemblage composition would be relatively straightforward and accurate if only abiotic variables operated as determinant factors. Although abiotic conditions clearly limit their distribution and occurrence, fish species are often absent from seemingly suitable and accessible habitats. Biotic interactions, in the form of competition or predation, may be of equal or greater importance than abiotic factors in structuring assemblages.

1.4.1 Competition

Patterns of resource partitioning among sympatric species are frequently interpreted as evidence of the importance of interspecific competition in communities (Schoener 1974; Ross 1986). Keast (1978; p. 7) found that fishes in Ontario lakes "differ in body size, morphology, abundances, habitats, diurnal and seasonal habitat utilization patterns, diets, dietary changes with age, reproductive strategies, and population turnover rates... that, by channeling their owners towards alternative resources, permit species to co-occur." Similar segregation was found among coexisting minnows in a northern Minnesota lake (Moyle 1973) and Lake Memphremegog (Gascon and Leggett 1977). Although suggestive, resource partitioning studies by themselves cannot provide strong support for the competition hypothesis if alternative processes have not been ruled out.

Stronger evidence is available when resource use patterns of species are observed to differ in the presence or absence of a potential competitor. Although still indirect, the interpretation of such 'niche shifts' can be relatively straightforward in the simplified fish assemblages of boreal lakes (Svärdson 1976). Several lakes in a region may contain only two fish species whereas other lakes contain just one of the pair. In these systems, the species often have similar patterns of habitat use, food habits, and/or growth when allopatric, but distinct patterns when they coexist (Nilsson 1965; Nilsson and Northcote 1981; Magnan and FitzGerald 1982;

Tonn et al. 1986; Tonn and Paszkowski 1987). In addition, differences in foraging behavior between species have been confirmed in laboratory experiments (Nilsson 1963; Schutz and Northcote 1972; Paszkowski 1985; Magnan and FitzGerald 1984; Tonn et al. 1986).

Manipulative field experiments, in which a potential competitor is added or removed and responses (niche shifts, changes in growth rates, density compensation) are quantified, also suggest that competition is important in structuring fish assemblages. For example, Fraser (1978) examined angler return, food habits, and growth rates of three salmonids stocked into a small lake in Algonquin Park, Ontario both before and after introduction of yellow perch (Perca flavescens). Yields of salmonids declined to 13% of pre-perch values, growth rates of the three species were significantly reduced, and the proportion of large food items (fish, leeches, Odonata nymphs) also declined following perch introduction. Fraser also noted that these significant competitive effects contrasted with the situation in nearby larger lakes, in which yellow perch coexisted at equilibrium with lake and brook charr (Salvelinus namaycush and S. fontinalis), suggesting that simplified habitat features and/or fish assemblages in small boreal lakes intensifies the effects of competition.

1.4.2 Predation

Selective predation can maintain relatively high local species diversity if it prevents dominant competitors from monopolizing resources (Paine 1974). However, within the boreal fish community literature little evidence exists for this phenomenon. Rather, predators usually alter species composition directly through complete exclusion of predation-intolerant species. Tonn and Magnuson (1982) suggested that large piscivorous species (largemouth bass and/or northern pike) excluded most small-bodied species (e.g., minnows) from small lakes of northern Wisconsin.

Tolerance of predation by populations of small fishes is aided by combinations of behavioral, physiological, and morphological adaptations. One strategy is complete avoidance, i.e., residency in an environment unavailable or unsuitable to the predator. For example, Svärdson (1976) suggested that a fish species that is easily preyed upon may develop tolerance for a severe abiotic environment where predation is low. As discussed above, many cyprinids and other small fishes are able to survive in lakes under severe conditions of winter hypoxia (e.g., Klinger et al. 1982; Magnuson et al. 1983, 1985; Holopainen and Hyvärinen 1985), and in the absence of intolerant piscivores, populations of these species thrive (Holopainen and Pitkänen 1985; Tonn and Paszkowski 1986).

Morphological anti-predator strategies include general characteristics, such as body size, and specific

characteristics like spines. Individual prey having a body size larger than the average predator gape will likely escape attack and thus maintain the population (Tonn and Paszkowski 1986). For example, golden shiners (Notemigonus chrysoleucas) appear to be better able to coexist with largemouth bass in Wisconsin lakes than other minnows because of their larger adult size (Rahel 1984). Likewise, many species of centrarchids have large adult body size; in addition, they possess well developed dorsal spines. These characteristics in combination may ultimately allow centrarchid populations to remain abundant within lakes containing pike and largemouth bass (Tonn and Magnuson 1982).

1.5 CONCLUSION

It is clear from the above discussion that for fish assemblages in small boreal lakes, both biotic and abiotic factors can contribute to fish assemblage composition. Furthermore, consistent interactions occur among biotic and abiotic factors which may result in repeatable and predictable patterns of fish assemblage structure.

2. FISH ASSEMBLAGES OF CENTRAL ALBERTA

2.1 INTRODUCTION

For fishery ecologists, the occurrence of repeatable local fish assemblages and their correlation with abiotic and biotic conditions of the lake in which they occur provide a vehicle for understanding and predicting how internal and external elements (e.g. eutrophication, species additions) influence and structure a lake's fish assemblage (Kerr 1982, Rigler 1982). However, studies that have successfully identified patterns in fish assemblage structure and related them to abiotic and biotic structuring mechanisms have been primarily restricted to regions (e.g., southern Ontario or northern Wisconsin) that are relatively similar, both environmentally and in terms of the richness and composition of their fish faunas. Can similar assemblage-level patterns be found and do similar assemblage-environment relationships exist in less species rich and environmentally different regions of northwestern North America?

Alberta's Athabasca River drainage basin has a relatively low total fish species diversity (35 species; Paetz and Nelson 1970) when compared to many areas of north-central North America (e.g., > 75 species in northern Wisconsin; Becker 1983). This low species diversity is thought to be due to a combination of large distances from

major historical glacial refugia (e.g., Mississippi Drainage; Lindsey and McPhail 1986) and climatic limitations (Shuter et al. 1980). Most of the central Athabasca drainage flows through woodland plains over muskeg-covered luvisolic, alkaline soils underlain by upper Cretaceous sandstone, shales and coal (Hardy 1967). As a result, most small lakes within this region differ from areas of north-central North America with respect to many limnological characteristics, such as nutrient levels, water color, and acidity (Chambers and Prepas 1988). It seems unlikely that some environmental factors identified as important in north-central North America (e.g., low pH in shield areas) are equally important in structuring assemblages in small Alberta lakes, whereas other factors (e.g., surface area) may have similar effects on Alberta assemblages because of a seemingly ubiquitous affect on vertebrate species composition (e.g., MacArthur and Wilson 1967).

To evaluate the general importance of previously identified influences on assemblages in small north-temperate lakes, I have determined the fish species composition and richness within small lakes of the central Athabasca River drainage and examined their relationships with environmental conditions of the lakes. Specifically, I addressed the following questions:

1. Are there discrete, repeatable assemblages of fish in these small lakes?

2. To what extent is the pattern of fish assemblage structure related to abiotic factors of the lakes' environment? Can these be linked with specific deterministic structuring mechanisms?
3. To what extent does piscivory contribute to assemblage structure?
4. How do the structuring mechanisms for fish assemblages in small lakes of central Alberta compare with those identified for lakes of north-central North America?

2.2 METHODS AND MATERIALS

2.2.1 Lake selection and sampling

Forty-five lakes under 100 ha in surface area were selected from accessible areas of the south-central portion of the Athabasca River basin (Figure 2.1-2.3). From May through August, 1986 and 1987, I determined fish species composition in each lake by using a combination of gear (Appendix I) set overnight. Fishes were identified to species (using Paetz and Nelson 1970), counted, and returned to the lake. A sample collection of each minnow species was retained to verify identification in the laboratory. Similar protocol has been shown to be effective in sampling fish assemblages

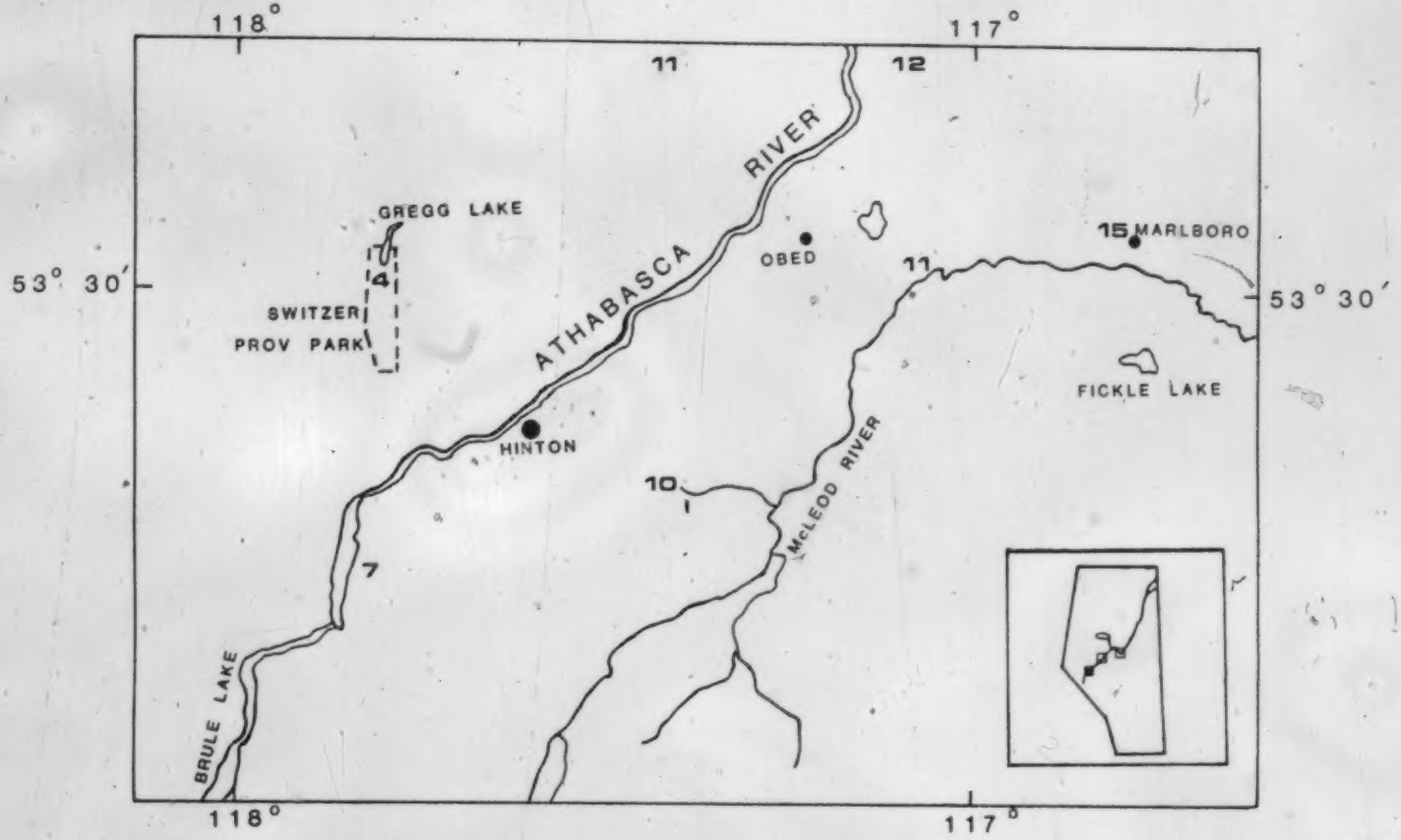

Figure 2.1. General location of study lakes in the Athabasca River basin near Hinton.

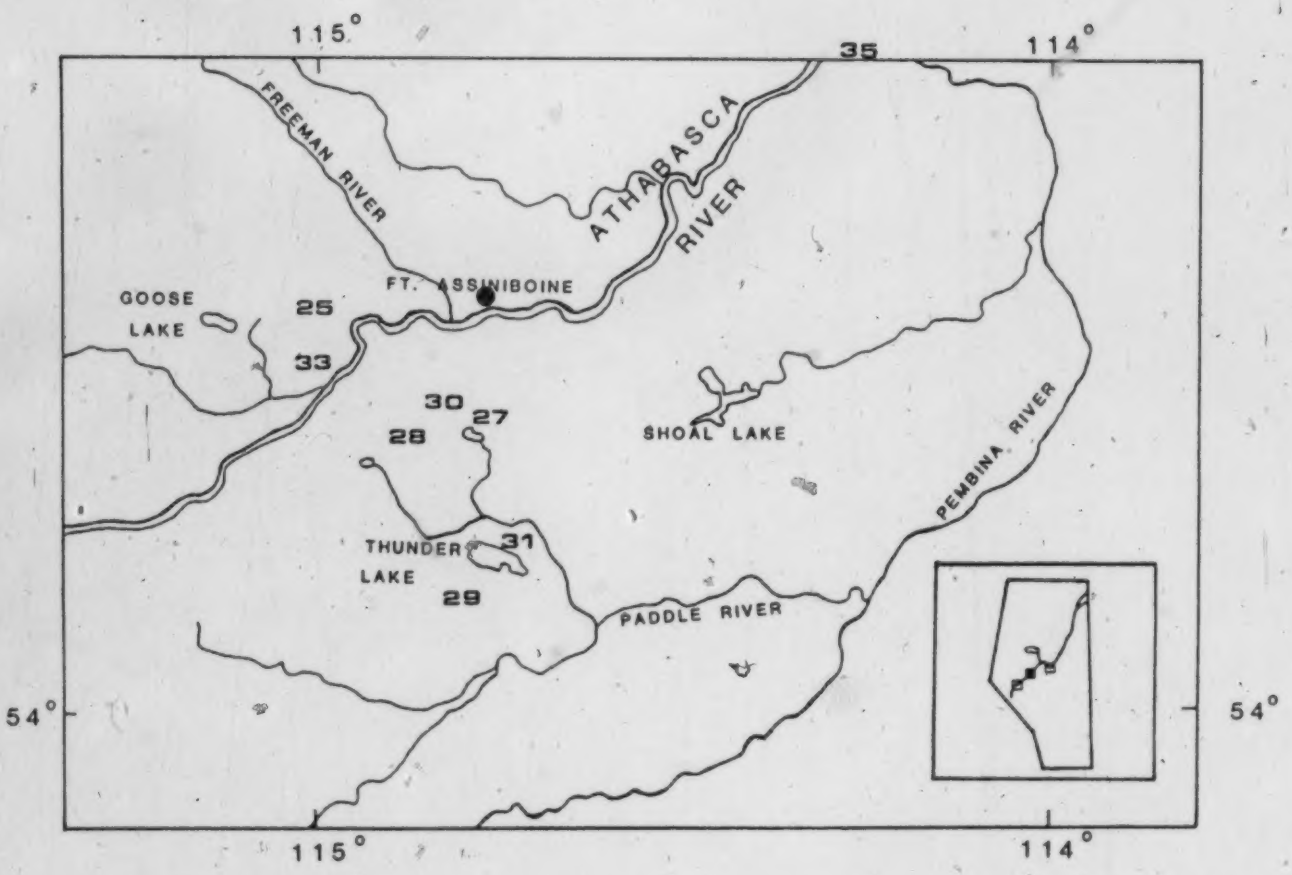

Figure 2.2. General location of study lakes in the Athabasca River basin near Ft. Assiniboine.

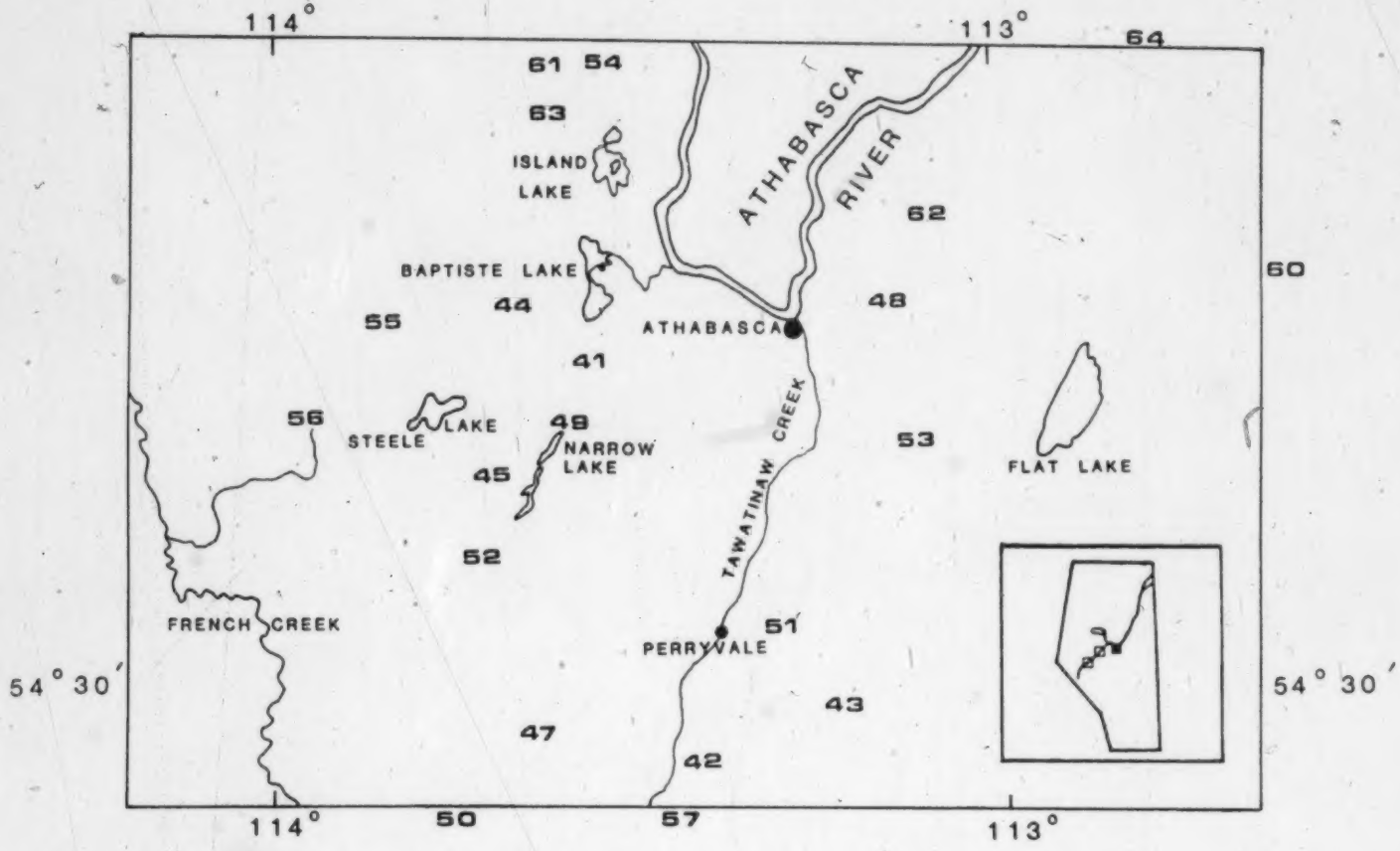

Figure 2.3. General location of study lakes in the Athabasca River basin near Athabasca.

in small lakes of other regions (Harvey 1981; Tonn and Magnuson 1982; Rahel 1984). However, to measure the repeatability of fish sampling for this set of lakes, a subset of six lakes was resampled, at various levels of intensity with the above gear, during May and August of 1986 and 1987.

For each lake, information was collected on several chemical and physical parameters (Appendix II). Conductivity and pH were measured in situ from vertical transects of at least six mid-water stations using a Hydrolab Surveyor II Water Quality Monitor. Depth and secchi depth were also determined at each station and depth at the deepest station was used as maximum depth. Water samples, collected from a depth of 0.5 meters at the center of a lake, were analyzed for apparent water color and total dissolved phosphorus using standard techniques of Alberta Environment and the Limnology Lab, University of Alberta (E.E. Prepas, unpublished guide, Dept. of Zoology, University of Alberta). Water samples and in situ measurements were collected once for each lake between 1100 and 1300 during July or August. For a subset of ten lakes I was able to compare my limnological measurements with results of an independent survey (E.E. Prepas, unpublished data). Surface area, shoreline length, and elevation were obtained from topographical maps (scale 1:50,000).

Macrophyte diversity and relative abundance (vegetation complexity) was estimated visually from grab samples at three

stations along each of six randomly placed transects running perpendicular to the shoreline. Isolation of a lake was quantified as follows: absence of an inlet/outlet (score: 0), presence of an intermittent inlet/outlet (score: 0.5), and presence of a permanent inlet/outlet (score: number of outlets X 2). I considered the presence of a permanent inlet/outlet to be much more important than an intermittent connection because of the increased potential for changes in assemblage structure due to immigration and emigration of fish species. Outlet information was obtained from 1:50,000 topographic maps (1974-76) and 1:100,000 county maps (1985-86) and, where possible, verified in the field.

2.2.2 General Approach to Pattern Analysis

Fisheries biologists have long been aware of the fact that certain fish species occur together in certain types of lakes. Until recently, it has been difficult to translate this knowledge, developed through experience, into a quantitative and objective framework. However, with the development of multivariate analysis, "effective, efficient, and appropriate" methods are available to summarize complex community-level data sets and reveal structural patterns (Gauch 1982). Multivariate community analyses mathematically measure similarities and differences among assemblages or lakes, based on their species composition or environmental characteristics. This provides an objective way for the

biologist to examine whether or not groups of similar assemblages exist that are distinct from other groups.

Multivariate analyses can also assist in ecological interpretation of revealed patterns by determining which species are important contributors to assemblage-level patterns or which environmental factors are most closely associated with different assemblage types. Conducting controlled manipulative experiments is often not feasible at the assemblage level. However, comparative studies, together with multivariate analyses, are frequently able to detect patterns, to generate and test hypotheses that assess the importance of different processes, and ultimately to produce acceptable explanations for community-level problems (Tonn et al. 1983; Diamond 1986).

To analyze for patterns of fish assemblage composition among small lakes of central Alberta, I subjected the lakes-by-species (presence/absence) data matrix to two methods of multivariate community analysis, hierarchical classification using agglomerative, unweighted group averaging and Jaccard's coefficient of similarity (Gauch 1982; Pielou 1984), and detrended correspondence analysis (DCA; Hill and Gauch 1980).

Environmental variables with fewer than three significant intercorrelations were retained for further analyses. This ensured that retained variables provided some independent description of an aspect of the lake environment.

Sequences of occurrence (Schoener and Schoener 1983) of the five most frequently occuring species were determined for each selected environmental variable. Lakes were ordered from lowest to highest value for each variable. The presence or absence of each species was recorded along this environmental gradient and the resulting pattern of presences or absences was tested for independence of distribution using the Mann-Whitney U test (Solkal and Rohlf 1981).

Canonical analysis (e.g., Berenson et al. 1983) was used to evaluate the extent to which groups of lakes (as described from classification and occurrence sequence analyses) are environmentally different. All environmental variables used in the analysis, except pH, were normalized by using a log 10 transformation. Canonical variates represent mathematical combinations of the environmental variables that maximize differences among groups of lakes relative to those within. I conservatively estimated the significance of group separation by visual inspection (after Green and Vascotto 1978). I also estimated the degree of group separation by analyzing the percentage of lakes correctly classified into an assemblage group according to the environmental classification functions. Scores of 100 percent indicate complete classification of lakes into a particular assemblage group (Berenson et al. 1983). Finally, the means of each lake group for each environmental variable were tested for significant differences using analysis of variance. Throughout this chapter, statistical significance will refer to $P < 0.05$,

unless otherwise stated.

2.3 RESULTS

2.3.1 Species Composition and Sampling Efficiency

Overall, 11 fish species were recorded in 36 lakes (Table 2.1); nine lakes were fishless. Brook stickleback (Culaea inconstans) was the most ubiquitous species caught. Because one lake contained only relatively rare coldwater species, burbot (Lota lota) and rainbow trout (Salmo gairdneri), it was considered to be ecologically distinct and excluded from further analyses.

Of the six re-sampled ponds, four showed no change in the number or composition of species present during 1986 and 1987 (Table 2.2). In Sara Lake, three Iowa darters (Etheostoma exile) were caught only on the second of four sampling dates, and were thus considered rare and not included as part of the Sara Lake assemblage. Gods Lake showed a doubling of species between May and August 1986, but stabilized in species composition by the end of the 1987 field season. This increase in species number was most likely related to unusually high precipitation during July 1986 that opened up an intermittent stream, allowing northern pike and white suckers (Catostomus commersoni) to invade. Because they

Table 2.1. The lakes by species (presence/absence) data matrix for the 36 lakes with fish. Lake numbers (Id) refer to those used on Figures 2.5 and 2.6. Species belong to a stickleback/fathead assemblage (st/fd), a northern pike/yellow perch assemblage (pike), or to a mixed species assemblage (mixed).

				Species											
Lake	Id	lat.	long.	bs	fm	np	ws	yp	fd	rd	pd	Id	bt	rt	Assem.
Mariana	64	55 50	112 06			1									pike
Teen	50	54 29	113 43			1									pike
Unnamed	30	54 14	114 44					1							pike
Gregg	04	53 39	117 41			1	1								pike
Unnamed	42	54 25	113 14			1	1								pike
Unnamed	25	54 19	114 59			1		1							pike
Jackfish	62	54 45	113 05			1		1							pike
Banana	55	54 43	113 50			1		1							pike
Lofty	60	54 43	112 29			1	1	1							pike
Crooked	54	54 55	113 32			1	1	1							pike
Ghost	63	54 52	113 35			1	1	1							pike
Jenkins	61	54 45	113 35			1	1	1				1			pike
Unnamed	49	54 38	113 35		1										bs/fm
Unnamed	27	54 13	114 45	1											bs/fm
Unnamed	28	54 05	114 42	1	1										bs/fm
Unnamed	29	54 12	114 28	1	1										bs/fm
Unnamed	31	54 06	114 47	1	1										bs/fm
Unnamed	43	54 26	113 08	1	1										bs/fm
Unnamed	45	54 39	113 38	1	1										bs/fm
Unnamed	11	53 31	117 40	1	1										bs/fm
Unnamed	33	54 17	115 03	1	1										bs/fm
Canoe	53	54 37	113 07	1	1										bs/fm
Unnamed	51	54 36	113 12	1	1										bs/fm
Unnamed	57	54 12	113 20	1	1										bs/fm
Spear	48	54 44	113 09	1	1										bs/fm
Unnamed	41	54 41	113 36	1	1		1								bs/fm
Unnamed	44	54 44	113 40	1	1		1								bs/fm
Sara	35	54 37	114 12	1	1				1	1					bs/fm
Petite	03	53 40	117 45	1	1				1	1	1				bs/fm
Unnamed	07	53 16	117 48	1					1	1					bs/fm
Emerson	12	53 44	117 50				1		1		1		1		bs/fm
Gods	47	54 24	113 39	1	1	1	1								mixed
Unnamed	52	54 32	113 41	1		1									mixed
Marlboro	15	53 33	116 50	1		1	1								mixed
Duck	56	54 38	113 57	1	1	1	1	1							mixed
Beaver	10	53 15	117 26										1	1	rare

bs: Brook stickleback, (Culaea inconstans), fm: Fathead minnow, (Pimephales promelas), np: Northern pike (Esox lucius), ws: white sucker (Catostomus commersoni), yp: Yellow perch, (Perca flavescens), fd: finescale dace (Phoxinus neogaeus), rd: Northern redbelly dace, (Phoxinus eos), pd: Pearl dace, (Semotilus margarita), Id: Iowa darter, (Etheostoma exile), bt: burbot (Lota lota), rt: Rainbow trout, (Salmo gairdneri).

Table 2.2. Species composition over time in a subset of six lakes where sampling was replicated in May and August, 1986 and 1987 (Blanks: no sampling done; Bs: brook stickleback, Fm: fathead minnow, Np: northern pike, Ws: white sucker, Yp: yellow perch, Id: Iowa darter, D: dace spp.).

	Sampling Date			
Lake	May '86	Aug '86	May '87	Aug '87
41	Bs,Fm,Ws	Bs,Fm,Ws	Bs,Fm,Ws	Bs,Fm,Ws
44	Bs,Fm,Ws	Bs,Fm,Ws		Bs,Fm,Ws
Sara	Bs,Fm,D	Bs,Fm,D,Id	Bs,Fm,D	Bs,Fm,D
Gods	Bs,Fm	Bs,Fm,Yp,Ws	Bs,Fm,Yp,Ws	Bs,Fm,Yp,Ws
Jenkins	Yp,Np,Ws,Id	Yp,Np,Ws,Id	Yp,Np,Ws,Id	
43	Bs,Fm	Bs,Fm	Bs,Fm	Bs,Fm

maintained populations for over a full year, both species were considered part of the Gods Lake assemblage. Based on the overall results of this resampling program, I concluded that the sampling protocol was consistent and efficient at catching susceptible species, and thus the results adequately represented the composition of a lake's assemblage.

2.3.2 Pattern Analysis

Hierarchical clustering of the 35 lakes with fish distinguished two major assemblage types at the 1% similarity level (Fig. 2.4). Detrended correspondence analysis of the lakes using species presence/absence (Fig. 2.5) also identified the two main assemblage types but, in addition, identified three lakes that had a mixed species composition. Each major assemblage type can be described by its more common and characteristic members: brook stickleback and fathead minnow (Pimephales promelas) versus northern pike and yellow perch. White suckers occurred twice as frequently in pike/perch lakes than in stickleback/fathead lakes whereas the three additional cyprinid species were restricted to the latter assemblage type (Table 2.1).

Occurrence sequence analysis of the five most common species indicated that yellow perch were found significantly more often in lakes that were deeper, larger in surface area, and lower in water color than lakes without perch (Table 2.3). Based on this result, I divided the previously

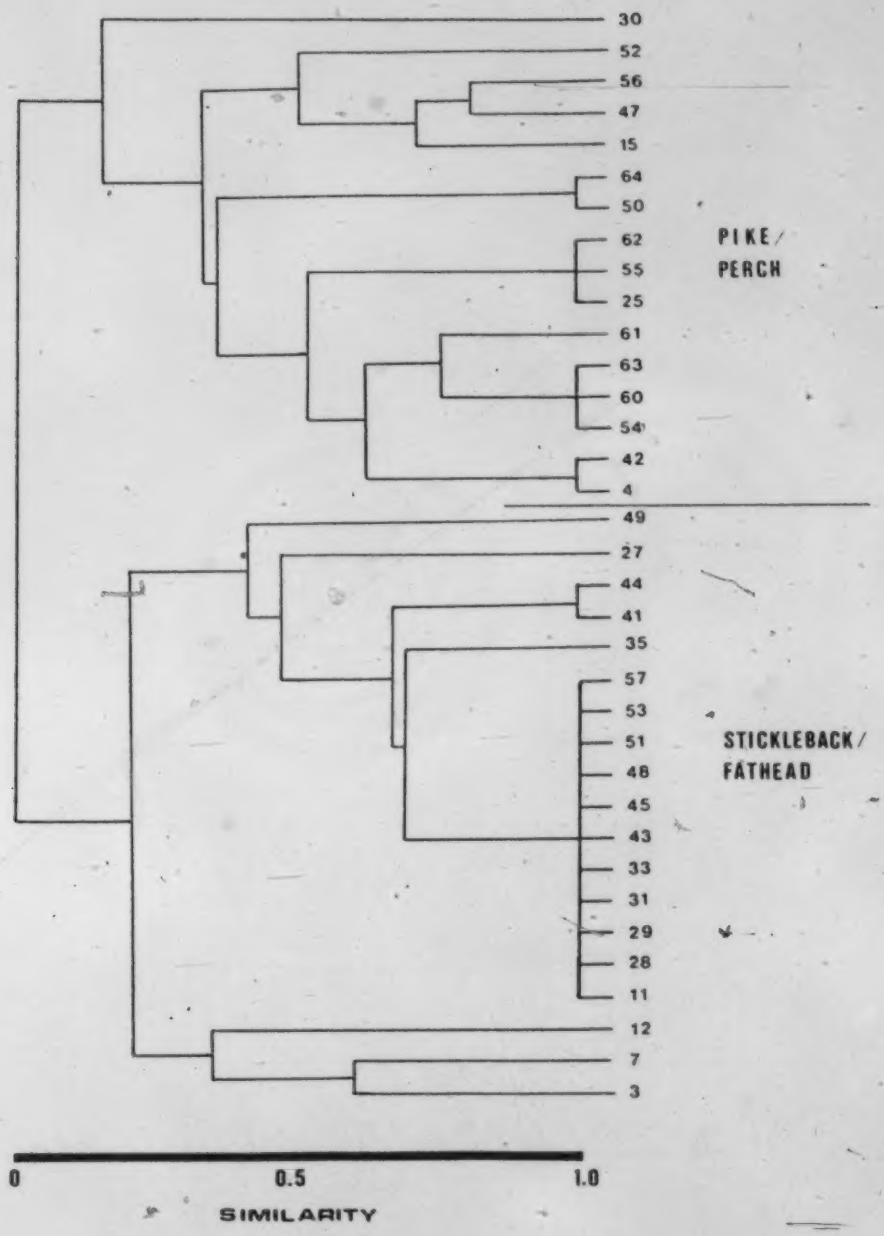

Figure 2.4. Hierarchical classification of 35 lakes with fish (excluding Lake 10), using Jaccard's coefficient of similarity and species presence/absence. (Numbers are Lake identifications as presented in Table 2.1).

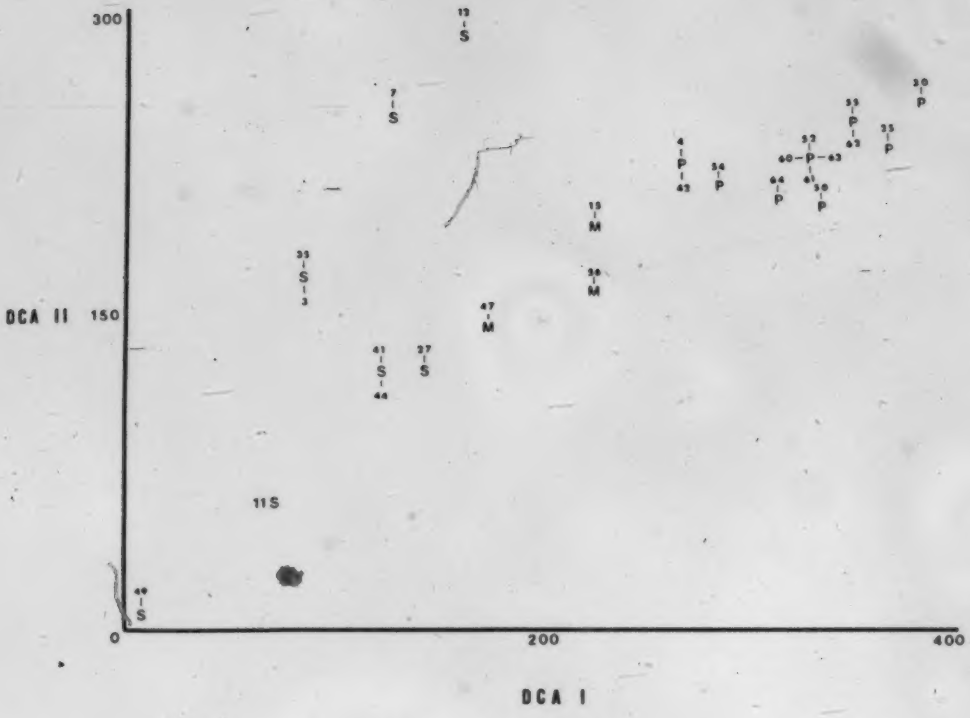

Figure 2.5. Detrended correspondence analysis of 35 lakes with fish. (Numbers around a symbol correspond to lakes in Table 2.1; Lake 10 is excluded and 11S refers to Lakes 11,28, 29,31,33,43,45,48,51,53, and 57). P: pike/perch assemblage, S: stickleback/fathead assemblage, M: assemblage consists of species from both S and P).

Table 2.3. Occurrence sequences for the five most common fish species along gradients of each of eight environmental variables. Species are classified as being concentrated at the low or high end of a gradient, or distributed throughout a gradient, based on Mann-Whitney U-tests of their patterns of presence and absence.

Environmental variable	Distribution of occurrence		
	low	throughout	high
conductivity		all 5 species *	
inlet/outlet		5 species	
maximum depth		4 species	perch
pH		5 species	
phosphorus		5 species	
surface area	bs & fm	2 species	perch
vegetation		5 species	
water color	perch	4 species	

* bs: brook stickleback, fm: fathead minnow, yellow perch, northern pike, white sucker.

identified pike assemblage into two sub-assemblages, namely, pike only (n=5) and pike/perch (n=8). Brook stickleback and fathead minnows were found significantly more often in lakes of small surface area. All five common species were distributed independently across gradients of lake isolation, pH, phosphorus concentrations, vegetation diversity, and conductivity.

To evaluate environmental distinctness of each assemblage type and fishless lakes, I applied canonical analysis to the matrix of the eight selected environmental variables (Appendix III). The three lakes with mixed assemblages, one lake with rare species, and three lakes with missing environmental data were excluded (n=38). The first two canonical variates, which accounted for 76% and 17% of the among-group variance, respectively, separated perch lakes from pike, stickleback/fathead, and fishless lakes (Figure 2.6). Classification of assemblage groups indicated that pike and stickleback/fathead lakes had the lowest (40% and 60% respectively), fishless lakes intermediate (75%), and perch the highest (88%) total percent correct classification. None of the misclassified stickleback/fathead, pike, and fishless lakes were misclassified as perch lakes. The misclassified perch lake was classified as a pike lake. Pike, stickleback/fathead, and fishless lakes did not differ significantly from each other with respect to any environmental variable considered individually (Table 2.4). All three did differ significantly from perch lakes with

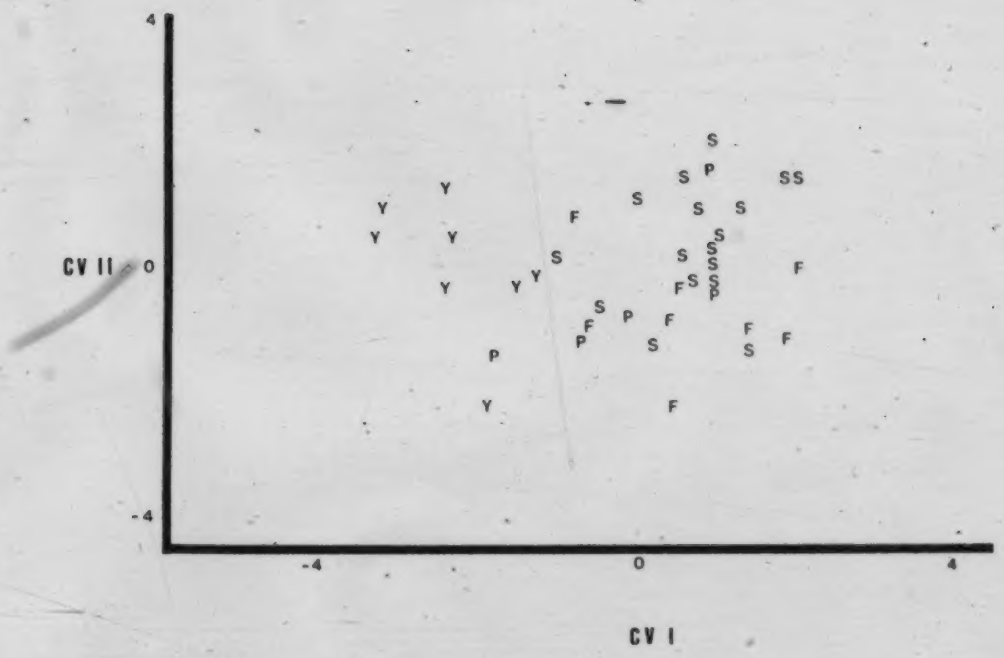

Figure 2.6. A graphic representation of a canonical analysis of 38 study lakes using eight environmental variables. Lakes were grouped into assemblage types (and fishless lakes) based on the results of classification, ordination, and occurrence sequence analyses. The three mixed assemblage lakes, one lake with rare species, and three lakes lacking complete environmental data were excluded from the canonical analysis. (S: Stickleback/ fathead, Y: yellow perch, P: northern pike, F: fishless lakes).

TABLE 2.4. Mean of each transformed environmental variable and pH, for the three assemblage types and for fishless lakes. The three lakes with mixed assemblages, one lake with rare species, and three lakes with environmental data missing, are excluded. The variables are presented in descending order of F values obtained from one-way ANOVAs (* $P < 0.05$, 3,35 d.f; bs/fm: brook stickleback/fathead minnow).

	Assemblage Type				
	bs/fm	pike	perch	fishless	F
# of lakes	17	5	8	8	
maximum depth (m)	3.19	4.23	8.99	2.38	* 7.79
surface area (ha)	15.92	19.52	65.63	15.64	* 4.63
pH	8.21	7.64	8.38	7.98	1.95
+ presence of inlet/outlet	0.39	0.52	0.64	0.11	1.73
water color (u pt/L)	22.32	31.85	18.46	37.23	1.05
++vegetation diversity	6.75	6.45	6.28	6.05	0.67
conductivity (uS/cm)	273.37	244.02	270.89	226.76	0.41
phosphorus (ug/L)	52.71	47.28	40.13	45.12	0.19

\+ 0: absent, 0.5: intermittent, 1.0: present
++ higher the number the greater vegetation diversity

respect to surface area and maximum depth. Overall, the results of the canonical analysis indicated that pike, stickleback/fathead, and fishless lakes show environmental similarity, whereas perch lakes are environmentally distinct. If stickleback/fathead, pike, and/or fishless lakes could occur at equal frequencies among the 30 environmentally similar small, shallow lakes (excluding the eight larger, deeper perch/pike lakes; refer to Table 2.4), then there are significantly more stickleback/fathead lakes, significantly fewer pike lakes and an expected number of fishless lakes ($G=7.56$, 2 d.f., $P < 0.05$).

2.4 DISCUSSION

Average fish species richness in small lakes of central Alberta was relatively low (2.4 species) compared with small lakes of Ontario (e.g., 10.6 species, Harvey 1981) and Wisconsin (e.g., 5.3 species, Tonn et al. 1983; 14 species, Rahel 1986). This result was not unexpected because of the great distance from major glacial refugia; (e.g., Mississippi River Basin, Lindsey and McPhail 1986) and an increase in climatic severity as one moves north. Despite low species richness, I was still able to identify two distinct fish assemblage types (brook stickleback/fathead minnow and northern pike/yellow perch).

The most readily apparent difference between the two main assemblages is the nearly perfect negative association

between pike/perch members and most members of the stickleback/fathead assemblage. Piscivores have been noted to alter assemblage composition in small boreal lakes through exclusion of predation intolerant species (Harvey 1981; Tonn and Magnuson 1982). As in north-central North America, exclusion was limited to small-bodied species, e.g., brook stickleback, fathead minnows, and dace species. The intolerance of these species to predation has largely been attributed to morphological traits (small maximum body size, and/or lack of spines), behavior, and physiology.

Species with relatively large adult body size can often coexist with piscivore populations whereas species lacking this size refuge do not (Tonn and Magnuson 1982). Rahel (1984) suggested that golden shiners are exceptions among small-lake cyprinids in Wisconsin; they are able to coexist with largemouth bass because of their capacity to attain a large body size. The large adult body size of white suckers may also contribute to their coexistence with pike in my study lakes and elsewhere.

Another morphological adaptation that can reduce predator effectiveness and thus aid in the coexistence with predators is the presence of spines (Hoogland et al. 1957; Reist 1980; Tonn and Magnuson 1982). Of the species caught in the study lakes yellow perch and brook sticklebacks possess dorsal spines that may act as protection against piscivory. Yellow perch may ultimately rely upon a combination of large adult body size and dorsal spines as mechanisms to increase

survival in the presence of northern pike. Even though sticklebacks coexisted with pike to a greater extent than similarly-sized but spineless cyprinids, it is unclear if stickleback spines alone provide protection from piscivory. This is particularly dubious in light of the small spines of Alberta sticklebacks (Nelson 1969) and the strong interaction between predator/prey size ratios and spine effectiveness (Reist 1980). Overall, increased coexistence with pike displayed by sticklebacks in the study lakes is most likely a result of combined effects of habitat use, behavioral responses to presence of pike (Reist 1980), and dorsal spines.

Fugitive species (Hutchinson 1951), lacking morphological adaptations and thus easily preyed upon, may develop adaptations allowing them to occupy marginal habitats (e.g., those having a severe abiotic environment) and use them as refuges if predators (or competitors) are physiologically excluded from these habitats (Svardson 1976). For example, sticklebacks and fatheads occurred most frequently and pike least frequently in small, shallow lakes that have the potential of frequently undergoing winter-kill (see also Tonn and Magnuson 1982; Henderson 1984).

Mixed assemblages may be exceptions in small Alberta lakes, but their species composition may reflect temporary conditions of the lake due to dynamic historic events. For example, Duck Lake contained a large population of pike but relatively few stickleback and fatheads. Perhaps predation by

recently immigrated pike had reduced but not yet eliminated these species populations or the presence of a permanent pike population has not allowed for the successful establishment of immigrant populations of sticklebacks and/or fatheads. The former event may be more plausible because local residents indicate that pike cannot overwinter in this shallow lake and historically pike have undergone a spring immigration from and a fall emigration to the nearby Athabasca River.

Another mixed assemblage lake (Marlboro) had an abundant population of both brook stickleback and pike, suggesting that some degree of coexistence is possible. In this lake stickleback were found to occupy areas under floating mats of vegetation. The ability to use vegetation and/or occupy a different microhabitat than that of the predator may allow small bodied species to coexist with predators, even in otherwise structurally simple habitats (Clady 1974; Tonn and Paszkowski 1987). However, continued coexistence in Marlboro Lake may also require periodic disturbance; local residents indicate that winterkill is historically frequent in this lake.

The effect of predation by pike on smaller bodied species in small lakes can be reasonably explained by combining knowledge of the environment with ecological and morphological characteristics of the prey. The absence of sticklebacks and fatheads from larger and more heterogenous study lakes, which are less isolated, contain abundant reproductive habitat and are abiotically more benign than

smaller lakes, may similarly be attributed to the combined predatory effects of perch and pike. Certain pelagic cyprinids (e.g., spottail shiner, Notropis hudsonius) co-occur with perch and pike in some larger lakes of the Athabasca drainage. As with brook stickleback in Marlboro Lake, this coexistence is likely due to reduced habitat overlap with piscivores. Overall, the results of this study suggest that small species common to small, shallow Alberta lakes are generally unable to exploit within-lake habitat refuges and are thus unable to coexist with piscivores.

The ordered sequence of occurrence of yellow perch along gradients of surface area and depth and the occurrence of pike in small, shallow lakes that are environmentally similar to stickleback/fathead lakes suggests that these latter three species are more tolerant of lower oxygen concentrations than yellow perch. Northen pike have been found to be better adapted than yellow perch for survival under simulated winterkill conditions (Petrosky and Magnuson 1972). Under natural conditions, pike can avoid conditions of winter hypoxia by emigration (Tonn and Magnuson 1982), altered under-ice distributions (Magnuson and Karlan 1970), and by increased ventilation rate and reduced movement (Petrosky and Magnuson 1972). Small bodied individuals and species have also been shown to be more tolerant of hypoxic conditions than larger fish because of reduced activity under the ice, head shape, and emigration (Casselman and Harvey 1975; Klinger et al. 1982; Magnuson et al. 1985).

Even though the component species in pike (without perch) and stickleback/fathead assemblages appear to have a similar tolerance for severe conditions associated with small, shallow lakes, significant differences in relative frequencies of each assemblage type were observed. The low frequency of pike and high frequency of sticklebacks/fatheads in small, shallow lakes may be related to the reproductive requirements of individual species (Scott and Crossman 1973; Rahel 1984). For example, the absence of vegetated, bays or marshes and the frequent absence of juvenile pike from the small, shallow lakes compared to large perch/pike lakes suggests reduced pike reproduction. However, I found an abundance of appropriate reproductive habitat in the small, shallow lakes that could allow sticklebacks and fatheads to maintain large populations.

The greater than expected occurrence of stickleback/fathead assemblages in small, shallow lakes may also be associated with the life-long possession of small bodies by stickleback/fathead members compared to northern pike, which are restricted to a similar body size (5-7cm) for only the first few months after hatching (Scott and Crossman 1973). Thus, small sized stickleback/fathead members may use dispersal avenues that remain available throughout the year (e.g., low surface run-off; Becker 1983), whereas pike may be restricted to dispersing during periods of high stream flow (e.g., spring spawning; Snow 1974). Overall, the combined effects of these and other factors suggest that small,

shallow Alberta lakes are more suitable for and available to sticklebacks/fatheads than northern pike.

Yellow perch, as a member of the pike assemblage, were limited to deeper, larger lakes in the study set. Lakes of this type may have a lower probability of winterkill (Magnuson et al. 1985) and have been associated with a greater abundance of prey and usable habitat (Eadie and Keast 1984). Elsewhere however, perch are frequently found in small, shallow lakes as well as larger, deeper lakes (Tonn and Magnuson 1982; Rahel 1984). Why are perch largely restricted to larger, deeper lakes in central Alberta?

Infrequent occurrence of perch in small, shallow Alberta lakes may ultimately be related to differences in combined effects of relative density, connectedness, and productivity of these lakes. The Northern Highlands district of Wisconsin contains a relatively high density of lakes, many of which have inlets/outlets, compared to Alberta. Alberta lakes are also considered to be far more productive than similarly sized Wisconsin lakes because of major differences in phosphorus source and retention (Riley and Prepas 1984). Because oxygen depletion and subsequent fish kills are positively linked with increased productivity (Barica 1975; Babin and Prepas 1985), shallow Alberta lakes may be subjected to more frequent and severe winterkill events than small lakes in north-central North America. High productivity coupled with greater relative isolation of small Alberta lakes may result in higher extinction rates, lower

colonization rates and reduced occurrence frequencies of perch. In Wisconsin, winterkill of perch is frequently incomplete; remnant perch populations (primarily juveniles) can survive and repopulate winterkill lakes (Tonn and Paszkowski 1986). Rapid re-colonization from nearby lakes is also more likely to occur.

The results of this study, combined with those from Wisconsin and Ontario, indicate that despite significant differences among regions, relatively few environmental variables appear to be important in structuring fish assemblages in small north-temperate lakes. In north-central North America, combinations of pH, surface area (and its correlate habitat diversity), depth (or winter oxygen concentrations), and lake isolation have frequently been noted as being most important in identifying or predicting lakes containing different types of fish assemblages and/or different levels of species richness (Johnson et al. 1976; Harvey 1975, 1978, 1981; Tonn and Magnuson 1982; Rahel 1984; Eadie and Keast 1984; Eadie et al. 1986). In Alberta, I similarily identified depth and surface area as important environmental factors related to assemblage composition.

Some studies have also identified productivity, or related factors, as being important in structuring fish assemblages in north-central North American lakes (e.g., Gascon and Leggett 1977), but I found no evidence that productivity, per se, influenced assemblage composition. Most of the species in the depauperate small-lake Alberta fauna

are quite generalized in their diets (Paetz and Nelson 1970), thus the limited effect of productivity-related factors may reflect the lack of more specialized species that are able to exploit additional resources available in more productive lakes.

In the lakes studied, pH ranged from 7.0-10.0, well above levels in most shield lakes (but comparable to off-shield lakes in Ontario; Harvey 1978, 1981). For most fish species, pH at this level is not physiologically stressful and thus should not play a major role in directly influencing assemblage structure. Somewhat more suprising is the relatively low importance in Alberta of factors associated with lake isolation (the presence and type of an inlet/outlet). An important difference between central Alberta and other regions where isolation plays a key role in structuring fish assemblages is the fact that a large proportion (70%) of my study lakes had intermittent inlets/outlets. The absence of historical data on flow regimes in these streambeds made it impossible for me to quantify the degree of stream intermittency. As a result, equal treatment of intermittent streams may have masked the true contribution made by lake isolation in structuring Alberta fish assemblages. Based on my observations, e.g, the appearance of pike and suckers in Gods Lake following a period of heavy rainfall, it seems likely that colonization or periodic recolonization of species can have important consequences to assemblage structure in small Alberta lakes.

In contrast to these environmental factors, piscivory appeared to be at least as important in structuring fish assemblages in Alberta as in north-central North America. The mutually exclusive or nearly exclusive co-occurrence patterns of northern pike and several smaller species was consistent with patterns in other regions and points to a widespread influence of the impact of predation on small-lake assemblage composition.

3. SURVIVAL OF SMALL-BODIED FISH SPECIES IN THE PRESENCE OF PIKE

3.1 INTRODUCTION

Many studies have identified major groups of environmental variables including lake severity, heterogeneity, isolation, and productivity (Harvey 1978, 1981; Tonn and Magnuson 1982; Tonn et al. 1983, Eadie and Keast 1984, Rahel 1986), that influence the species richness and composition of fish assemblages in small lakes of northern North America. The results of these studies indicate that fish assemblage composition and richness would be accurately predicted if environmental variables were solely responsible for their structure. In many regions however, some species are absent from accessible and environmentally suitable lakes (Harvey 1981, Tonn and Magnuson 1982). One explanation for such absences is the action of biotic processes, such as competition and predation.

The role of interspecific competition in structuring fish assemblages in small northern lakes has been investigated by examining population size and structure (Moyle 1973; Gascon and Leggett 1977; Tonn 1985), resource use patterns (Nilsson and Northcote 1981; Tonn and Pazkowski

1987), and individual growth and reproduction (Fraser 1978; Persson 1986). Interspecific competition does not generally prevent species from occupying a lake but affects the aforementioned traits of competing species (Henderson 1984).

Another biotic process, predation by piscivores, may have a more direct effect on structuring assemblages in small lakes by excluding populations of predation-intolerant species, particularly cyprinids (e.g., Harvey 1981; Tonn and Magnuson 1982; Rahel 1984). These species may be absent from lakes with specialized piscivores because of their small body size (Rahel 1984) and/or their lack of spines (Tonn and Magnuson 1982).

However, species that have a large adult body size, which can serve as a refuge from piscivory (e.g., golden shiner; Rahel 1984), must pass through smaller body sizes that are potentially susceptible to predation (Becker 1983). Also, the presence of spines on small fish may be a very limited deterent to predation from large piscivores (Reist 1980). Reist suggested that for large (>18 cm) northern pike, the morphology of brook sticklebacks is irrelevant and escape behavior, initiated before contact, will be favored. Potential similarities in body size and ineffectiveness of protective morphology suggests that other mechanisms may influence survival of small bodied fishes. The main objectives of this study were to experimentally determine survival rates of similarly sized fishes in the presence of a piscivore and to determine what species characteristics may

be responsible for differential survival. Specifically, I analyzed survival of yellow perch, brook stickleback, fathead minnow, and finescale dace (Phoxinus neogaeus), alone and in all possible species combinations, in the presence of northern pike.

3.2 METHODS AND MATERIALS

All experiments were performed at Meanook Biological Research Station, Athabasca, Alberta. For all experiments, survival was defined operationally as the ability of individuals to live through a 48 h encounter with a single pike.

Northern pike (25-35 cm total length), minnows, sticklebacks, and juvenile perch were collected by beach seine from local lakes. Predator and prey fishes were held in separate tanks (1.5 in diameter by 0.5 m deep). Pike were fed northern redbelly dace (Phoxinus eos), and prey species were fed Nutrafin flaked fish food and/or frozen brine shrimp.

Seven pike were randomly selected from the holding tank and placed individually into one of three 1.23 m X 0.5 m X 0.6 m or one of four 0.92 m X 0.5 m X 0.6 m tanks. Pike were allowed to acclimate to test tanks for 3 d and were not fed. In all experiments, I used prey 55-65mm total length to provide the 25-35cm pike with optimally sized prey (Hart and

Connellan 1984).

I conducted predation experiments for each species singly and for all pair-wise, three-way, and four-way species combinations. Ten replicates of each experiment were performed. A trial began when 24 individual prey (equally divided among species in a combination) were introduced to a tank containing a restrained pike. After about 5 min, the pike was released and allowed to feed until all individuals (single species experiments), approximately 50% (pair-wise), 33% (three-way), or 25% (four-way) of the prey individuals were eaten, up to a maximum of 48 hr. Individual prey that died (but not eaten) during a trial were removed and replaced. Prey were not fed during experiments.

For each multi-species experiment, I assumed *a priori* that there was equal survival across all species and tested for heterogeneity and goodness-of-fit of prey survival using G-tests (Solkal and Rohlf 1981). The heterogeneity G tests whether or not the results of the individual trials in an experiment are uniform whereas the pooled G indicates the degree of deviation of the combined results of all trials in an experiment from the expected equal survival ratio. I also tested for differences in mean numbers of individuals surviving among species within each species combination and among species combinations within each species using t-tests and one-way analyses of variance. Statistical significance will refer to $P < 0.05$, unless otherwise indicated.

3.3 RESULTS

In single species trials, perch had a significantly higher mean survival than the other species in each of five 12 h blocks; all perch individuals were eaten within 60 h from the start of a trial. Survival of dace and sticklebacks did not differ significantly for the first four 12 h blocks, but both species survived significantly better than fatheads and remained up to 48 h. Fathead minnows had the lowest overall percent mean survival, becoming extinct within 36 h (Fig. 3.1).

G-tests for heterogeneity indicated that the ten replicate trials for each series of pair-wise, three-way, and four-way experiments did not differ significantly from each other (Table 3.1). Thus, I combined trials for a particular experiment and analyzed the pooled G statistics.

Only one species pair-wise combination (stickleback/dace) failed to show significant differential survival (Table 3.1 and Fig. 3.2). Inspection of individual trials of the stickleback/dace experiment (Appendix IV) indicate that in five trials sticklebacks experienced greater survival than dace, in four trials dace had greater survivorship, and in one trial species survived equally. This result is consistent with single species trials in that there was not a significant difference between the mean number of dace versus stickleback individuals surviving a 48 hr

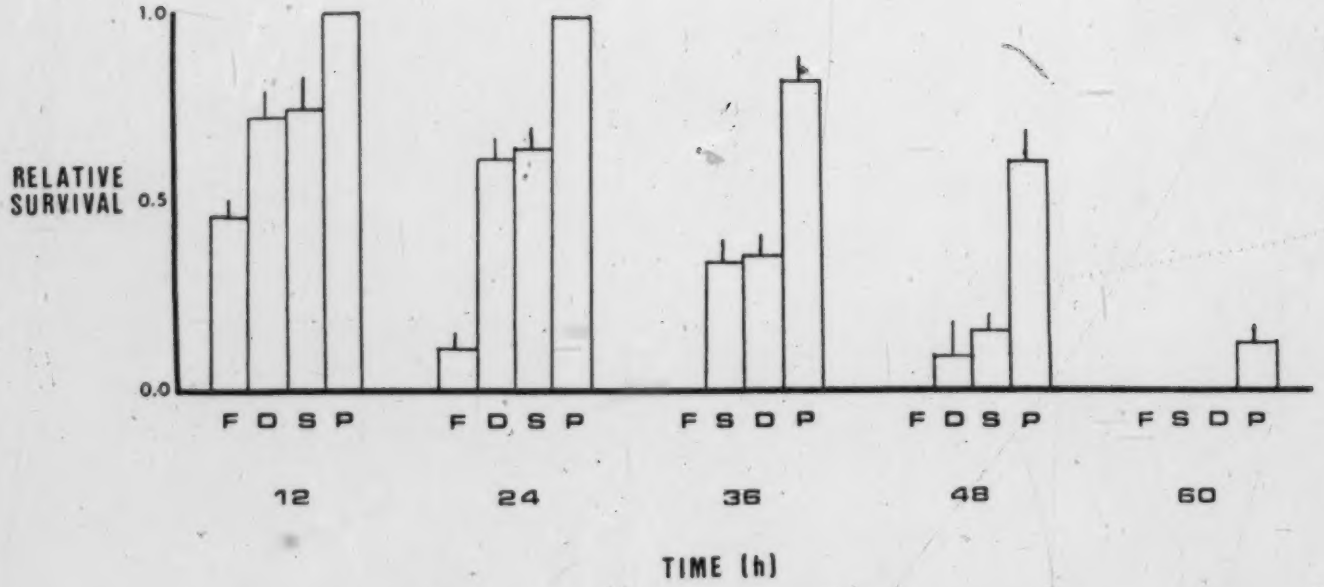

Figure 3.1. Mean relative survival (and standard deviation) of four prey species tested independently, in each of five 12 h blocks. For each block, relative survival is presented in increasing order as the number of individuals surviving divided by the total number presented (n=24). All non over-lapping means are significantly different; tested using ANOVA of original data arcsin/square root transformed, $P < 0.05$ (F: Fathead minnow, D: Finescale dace, S: Brook stickleback, P: yellow perch).

Table 3.1. Results of G tests analyzing the goodness-of-fit and heterogeneity of 10 trials of each possible species combination. The heterogeneity G measures the uniformity among the 10 trials whereas the pooled G measures the degree of deviation of all trials combined from the expected survival ratio (pair-wise 1:1, three-way, 1:1:1, four-way 1:1:1:1; Bs: Brook stickleback, Fm: Fathead minnow, Fd: Finescale dace, Yp: Yellow perch).

Species Combination	Pooled G	Hetero. G
Bs/Fm	20.39 **	07.56
Bs/Fd	00.01	11.16
Fm/Yp	43.25 **	03.90
Fm/Fd	10.60 **	04.73
Bs/Yp	35.51 **	02.18
Fd/Yp	17.09 **	12.32
d.f.	1	09
Bs/Fd/Yp	17.30 **	13.89
Fm/Fd/Yp	13.73 **	03.86
Fm/Fd/Bs	28.02 **	03.54
Fm/Yp/Bs	25.07 **	04.57
d.f.	2	18
Bs/Fm/Fd/Yp	15.10 **	04.09
d.f.	3	27

** P<< 0.01
d.f.: degrees of freedom

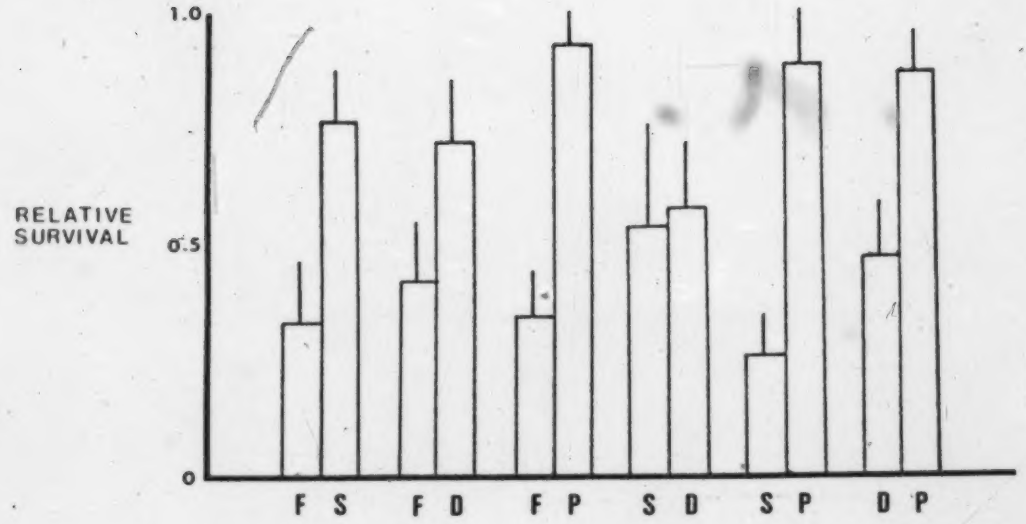

Figure 3.2. Mean relative survival (and S.D.) of four prey species over 48 hr, in the presence of pike, in all possible pair-wise species combinations. Relative survival for a species combination is presented in increasing order and as the number of individuals surviving divided by the total number presented (n=24). All non over-lapping means are significantly different; tested using t-tests of original data, $P < 0.05$ (F: Fathead minnow, D: Finescale dace, S: Brook stickleback, P: Juvenile yellow perch).

encounter with northern pike (Fig. 3.1).

Analysis of species mean survival across each pair-wise experiment indicated that sticklebacks had significantly higher survival when combined with a cyprinid than with perch (Table 3.2 and Fig. 3.2). Likewise, survival of dace was significantly higher when paired with fatheads than with perch, but the former survival rate did not differ from survival with sticklebacks. Fathead minnows showed low survival regardless of the species pair-wise combination, whereas perch showed high survival regardless of the other species with which they were paired (Table 3.2 and Fig. 3.2).

Survival patterns for each of the three species combinations differed significantly from an expected survival ratio of 1:1:1 (Table 3.1 and Fig. 3.3). Perch had significantly higher mean survival than other prey in each species combination (Fig. 3.3). Among remaining species, mean survival was strongly dependent upon the species combination. Fathead survival was significantly lower when sticklebacks were present than when the latter were absent and dace present. Dace survival was significantly lower with perch than without (Table 3.2). When the number of individuals of each species surviving versus the number eaten is compared among pair-wise and three-way experiments using a 2 X 2 contingency test, only perch showed a significant increase in the proportion of individuals surviving in three-way experiments ($G = 21.803$, $P < 0.01$).

Table 3.2. Mean survival (number of individuals) of each species in the presence of pike, across all possible pair-wise and three-way combinations. For each combination, differences between means were tested using ANOVA. Means not significantly different are joined with bars. (Refer to Fig. 3.2 and 3.3; Fm: Fathead minnow, Bs: Brook stickleback, Fd: Finescale dace, Yp: Yellow perch).

	Species Combination		N	Mean (# ind)	Var.	(P < 0.05)
+	Fm	Bs	10	04.00	3.11	| |
		Yp	10	04.00	1.33	| | |
		Fd	10	05.20	3.29	
	Bs	Yp	10	03.00	1.11	
		Fd	10	06.70	5.79	|
		Fm	10	09.10	2.09	
	Fd	Yp	10	05.20	4.84	|
		Bs	10	06.80	2.84	|
		Fm	10	08.60	2.71	
	Yp	Fm	10	10.20	0.62	| |
		Fd	10	10.30	1.34	| |
		Bs	10	10.40	1.38	
*	Fm	Fd Yp	10	02.30	0.23	|
		Bs Fd	10	02.40	0.71	
		Yp Fd	10	04.10	0.98	
	Bs	Fm Fd	10	03.50	1.17	|
		Yp Fd	10	05.10	2.67	|
		Yp Fm	10	05.30	0.23	
	Fd	Bs Yp	10	03.50	4.98	|
		Yp Fm	10	04.80	1.56	
		Fm Bs	10	07.10	0.54	
	Yp	Fm Fd	10	07.40	0.49	| |
		Bs Fm	10	07.70	0.23	| |
		Bs Fd	10	07.80	0.18	

\+ 12 individuals of each species offered
* 08 individuals of each species offered

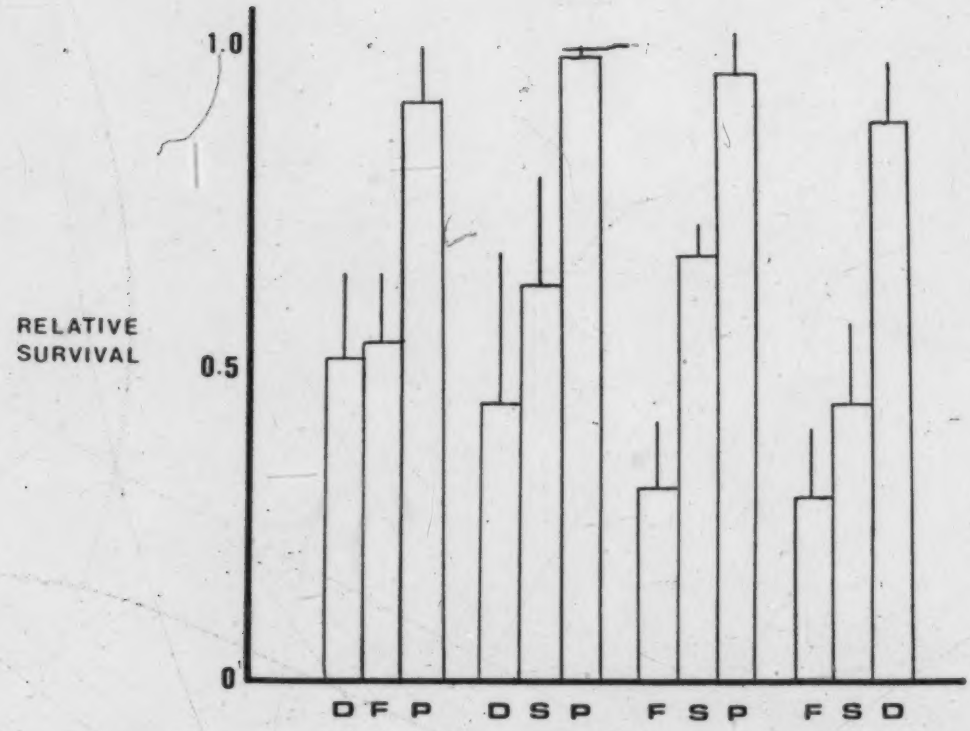

Figure 3.3. Mean relative survival (and S.D.) of four prey species over 48 hr in the presence of pike, in all possible three-way species combinations. Relative survival for a species combination is presented in increasing order and as the number of individuals surviving divided by the total number presented (n=24). All non over-lapping means are significantly different; tested using ANOVA of original data, $P < 0.05$ (F: Fathead minnow, D: Finescale dace, S: Brook stickleback, P: Juvenile yellow perch).

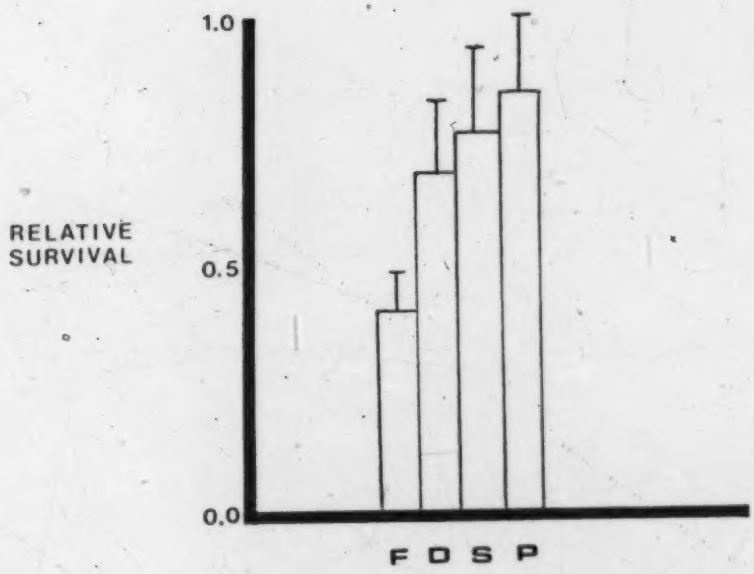

Figure 3.4. Mean relative survival (and S.D.) of four prey species over 48 hr in the presence of pike, in the four-way species combination experiment. Relative survival is presented in increasing order and as the number of individuals surviving divided by the total number presented (n=24). All non over-lapping means are significantly different; tested using ANOVA of original data, $P < 0.05$ (F: Fathead minnow, D: Finescale dace, S: Brook stickleback, P: Juvenile yellow perch).

When all species were available simultaneously, survival was significantly different from an expected survival ratio of 1:1:1:1 (Table 3.1). However, only fatheads showed significantly lower mean survival than the other three species ($F=31.16$, 3, 37 d.f., $P < 0.01$; Fig. 3.4).

3.4 DISCUSSION

The ordering of species survival in pair-wise, three-way, and four-way experiments was generally consistent with differential survival among the four prey species tested individually. Generally, perch had the greatest, sticklebacks and dace intermediate, and fatheads the lowest survival. Differential survival may have been a result of innate predator preference and/or behavioral or morphological characteristics of the prey.

Qualitative observation and comparisons with similar studies strongly suggest that the most susceptible species, fathead minnow, was most accessible to northern pike. Loose, constantly-moving groups of fatheads tended to concentrate off the tank bottom, in close proximity to a resting pike (see also Mauck and Coble 1971). Because northern pike rely heavily upon vision for prey capture (Hoogland et al. 1957; Christiansen 1976), low fathead survival was probably due to the swimming pattern of fatheads (continual changes in

direction), which may have offered frequent and strong visual stimuli that would illicit a predatory response (Webb and Skadsen 1980).

In contrast, perch survival may have been highest due to a combination of morphology (dorsal spines), reduced movement, and their location high in the water column along tank sides. Moody et al. (1983) describe very similar laboratory behavior and distributions for bluegill and fatheads in the presence of tiger muskellunge (Esox species). They concluded that low bluegill and high fathead susceptability was due to avoidance behaviors, escape tactics, and tank distributions.

Generally, dace and sticklebacks exhibited similar intermediate survival when compared to fatheads and perch. However, dace tended to aggregate at the water surface, potentially reducing their frequency of encounter with pike which remained on the bottom of the tank. In contrast, sticklebacks which also remained on the bottom of the tank, were observed to frequently remain motionless or move very little, thus potentially offering few visual strike cues for pike (Webb and Skadsen 1980). These qualitative differences suggest that these species may use different strategies to obtain similar survival rates in the presence of pike. Further testing is required to quantitatively determine the mechanisms used by dace and sticklebacks to produce similar intermediate level of survival relative to perch and fatheads.

Changes in a species' survival can be dependent upon the identity of associated species (Mauck and Coble 1971). For example, when dace were present with fatheads, the latter species tended to shoal with the dace near the water surface. This reaction may have increased fathead survival (though not significantly) by reducing the frequency of encounter with pike and because safety from predators increases by associating with a larger shoal (Godin and Morgan 1985; Morgan and Colgan 1987). Even though the resulting mixed species shoal would potentially be more vulnerable to predation than a single species shoal (Allan and Pitcher 1986), dace survival was also higher when fatheads were present than when they were absent. In the experiments where dace were absent, fatheads continued to aggregate near the tank bottom thus maintaining a high frequency of encounter with pike and a low overall survival.

A trend in the species combination experiments is the overall lower survival of the spineless cyprinids when combined with species with spines. However, one exception occurs when sticklebacks are combined with the two cyprinids. In this experiment, mean dace survival increases significantly when fatheads and sticklebacks are both present relative to when only one or the other latter species is combined with dace and perch. In contrast, the survival of the both fatheads and sticklebacks is significantly lower when combined with dace relative to their survival in at least one of the other three-way species combinations with

perch (Table 3.2). The exact mechanism for this result is unclear but fatheads may react to the presence of sticklebacks more readily (i.e. by moving to them) than to dace. This seems plausible because in small lakes of central Alberta, it is very common to catch sticklebacks and fatheads in the same traps. I found that when dace are present in a lake they are usually taken in association with other dace species and rarely with fatheads or sticklebacks.

Overall, fathead survival is basically unaffected by the presence of different species (in pair-wise experiments), or increases when they are combined with the other spineless cyprinid. The association of more vulnerable fatheads with sticklebacks and/or dace may ultimately result in reduced survival of the latter species. Whether this change in species survival is a function of the response of the prey or a function of the predator has not been determined.

The results of these experimental prey species manipulations compare favourably to survival of the prey observed in natural environments. In many small northern boreal lakes yellow perch frequently occur with northern pike (e.g., Harvey 1978,1981; Tonn and Magnuson 1982; Rahel 1984). In contrast, brook stickleback occur only slightly more frequently than fathead minnows and finescale dace, both of which rarely occur in the same lakes as northern pike. Even though the mechanisms responsible for differential survival were not identified, these experiments give support to the hypothesis that piscivory is responsible for maintaining an

exclusive occurrence of piscivores and spiney fishes versus predation-intolerant small-bodied species. It is important to remember that in natural systems, environmental complexity, life history patterns, and habitat use, among other factors, also play major additional roles in influencing the coexistence of various species.

4. GENERAL CONCLUSIONS

The results of this study support and extend results from other regions in demonstrating that aspects related to environmental severity (maximum depth), habitat heterogeneity (surface area) and, to a lesser extent, isolation (presence and type of inlet/outlet) have widespread influence in structuring fish assemblages in small north-temperate lakes. Identification of a small number of local environmental factors that influence fish assemblages in several north-temperate regions may be, in part, due to inherent characteristics associated with the insular nature and structural simplicity of small lakes and their conservative responses to common aspects of the north-temperate climate. In contrast, regional factors such as edaphic influences on productivity and water chemistry (pH), the relative isolation of Alberta from glacial refugia, and the generalized nature of the Alberta fish fauna may have minimized the richness of individual assemblages, the number of distinct assemblages and/or the discriminatory power of the analyses, relative to other regions of North America.

The influence of piscivory in structuring small Alberta lake assemblages was also consistent with that observed in north-central North America. The strong, direct, assemblage-level effects of piscivory on these systems may be related to small population sizes and/or simple lake habitats in combination with the presence of small, vulnerable species. The laboratory experiments performed, strongly

support the hypothesis that piscivory is largely responsible for the assemblage-level patterns observed. Overall, this study, based in a region of northwestern North America hundreds of kilometers from where previous studies of fish assemblages in small lakes have concentrated, clearly reveals that the structure of these assemblages bear the imprints of both local and regional influences.

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Appendix I. Type of fish sampling gear used in each of the 45 lakes included in this study. Traps and nets were left in a lake for 18 to 24 hours, including overnight.

Gear type	Dimensions	Number	Location in pond
Minnow trap	44.5 cm long 23 cm diameter	40	unbaited, in pairs on bottom
Fyke nets	4 m x 1 m lead 0.6 cm mesh 76 cm hoops	5	perpendicular to shore
Gill nets	38 m long 1.8 m deep panels: 1.3, 1.9,2.5,3.1, 8.1 cm mesh	2	parallel to shore in 2m of water *
Trammel net	37 m long 1.2 m deep 20 cm walls 2.5 cm mesh	1	parallel to shore in 2m of water *
Beach seine	8 m long 5 mm mesh	1	6 15 minute seines on hard bottomed areas *

* if available

Appendix II. Physical and chemical limnological information collected for each of the 45 study lakes sampled in Alberta.

CHEMICAL MEASUREMENTS	PHYSICAL MEASUREMENTS
* Total dissolved phosphorous	* maximum depth
* Apparent water color	* surface area
* conductivity	shoreline length
* pH	altitude
secchi depth	* inlet/outlet
	* Vegetation: macrophyte diversity macrophyte abundance

* Selected for further evaluation in species occurrence sequences and canonical analyses.

Appendix III. Morphometric and limnological characteristics of the 45 lakes sampled within the Athabasca River Basin. Refer to Table 2.1 for species compostition and lake name. (Blanks: no data collected).

	Id	pH	Color (µpt/L)	Cond (µS/cm)	Max z (m)	Surf A (ha)	Veg*	Phos (µg/L)	Inlet**
	003	8.20	002.50	197.00	04.00	011.25	05.00	013.90	0.00
	004	7.90	012.50	321.00	04.50	006.43	07.00	026.00	2.00
	007	8.70	010.00	458.00	03.00	010.83	06.00	021.30	0.50
	011	8.00	050.00	255.00	01.50	003.75	05.00	019.10	0.50
	012	7.82	050.00	317.00	07.25	007.50	06.00	016.30	0.50
	025	7.30	010.00	300.00	07.00	051.25	07.00	050.00	0.50
	027	7.50	006.00	282.00	02.00	007.50	07.00	058.00	0.50
	028	7.65	015.00	484.00	02.75	025.00	08.00	045.00	0.50
	029	8.33	030.00	370.00	03.00	030.20	07.00	065.00	0.50
	030	8.05	015.00	364.00	07.00	028.75	06.00	024.00	0.50
	031	8.09	020.00	380.00	03.00	024.17	08.00	030.00	0.50
	033	8.00	010.00	415.00	07.00	043.33	06.00	040.00	0.50
	035	8.50	010.00	215.00	06.00	090.00	08.00	029.30	0.50
	041	8.10	030.00	330.00	09.00	007.50	07.00	036.50	0.50
	044	9.10	100.00	080.00	01.50	029.20	06.00	080.00	0.50
	050	7.81	025.00	270.00	08.40	036.25	07.00	028.00	0.00
	052	8.00	070.00	260.00	04.00	016.25	06.00	048.00	0.50
	055	8.10	010.00	212.00	16.70	057.50	06.00	016.40	2.00
++	061	8.97	015.00	261.00	13.00	090.00	06.00	026.00	4.00
++	062	8.20	020.00	210.00	06.00	085.00	06.00	021.40	0.00
	063	8.60	020.00	293.00	13.00	095.00	06.00	049.00	0.50
++	054	9.20	050.00	260.00	07.40	080.00	09.00	057.00	6.00
	042	7.68	050.00	400.00	02.00	012.00	08.00	100.00	2.00
	043	8.15	040.00	236.00	01.75	018.00	11.00	086.30	0.50
	048	9.03	007.50	174.00	02.00	010.00	06.00	041.10	0.50
	049	7.50	100.00	248.00	04.60	003.75	07.00	074.00	0.50
	051	8.10	040.00		01.50	014.00		070.00	0.50
	053	9.30	040.00	417.00	02.40	100.00	08.00	500.00	0.50
	057				02.50	062.50	08.00		0.50
	060	8.60	030.00	300.00	07.00	070.00	05.00	172.00	0.50
	064	6.82	030.00	096.00	04.50	062.50	06.00	060.00	2.00
	045	7.70	070.00	190.00	02.70	010.00	06.00	360.00	0.50
+	100	8.12		235.00	01.75	002.50	05.00		0.50
+	101	8.30	007.50	254.00	01.75	100.00	06.00	020.40	0.50
+	102	7.50	070.00	115.00	01.75	002.50	04.00	015.90	0.00
+	103	8.00	055.00	315.00	02.50	010.00	06.00	119.00	0.00
+	104	8.18	020.00	289.00	06.75	020.00	06.00	036.00	0.00
+	105	7.90	100.00	139.00	01.00	042.50	07.00	065.00	0.50
+	106	6.78	040.00	157.00	02.00	042.50	10.00	040.00	0.50
+	107	8.10	020.00	453.00	10.00	006.25	06.00	045.00	0.50
+	108	9.13	080.00	266.00	01.00	006.25	05.00	085.00	0.50

\+ fishless lake
++ data collected from discrete basin within lake.
* higher number = greater macrophyte divesity/abundance.
** 0: absent, 0.5: intermittent, x/2: number of inlets/outlets.

APPENDIX IV. Survival data from all possible prey species combinations in the presence of pike (Refer to Chapter 3).

Pair-wise Experiments:

Bs	Fm	Bs	Fd	Bs	Yp	Fd	Fm	Fd	Yp	Fm	Yp
6	5	8	6	1	12	12	4	7	9	6	12
10	3	9	6	3	9	8	3	5	9	4	11
11	4	5	8	4	11	9	3	5	10	5	11
9	1	6	6	3	8	8	7	0	12	3	10
9	3	3	10	2	11	8	5	5	9	2	12
8	5	4	8	3	11	8	7	5	11	4	12
10	5	9	6	4	11	11	7	4	12	3	10
10	2	8	6	2	11	7	3	6	10	4	11
10	5	10	4	4	10	7	6	7	10	4	12
8	7	5	8	4	10	8	7	8	11	5	11

Three-way Experiments:

Fm	Yp	Fd	Bs	Yp	Fd	Bs	Yp	Fm	Bs	Fm	Fd
4	7	4	4	8	6	5	8	2	3	3	7
6	7	6	7	8	5	5	8	2	4	2	6
3	8	3	7	8	5	6	7	3	2	2	8
3	7	5	4	8	1	6	7	4	3	2	7
4	7	3	7	8	2	5	8	1	6	2	7
5	8	3	5	8	1	5	8	3	4	2	6
5	8	5	3	8	5	5	7	2	3	2	7
4	6	2	4	7	6	6	8	2	3	2	8
3	8	4	3	8	1	5	8	3	4	3	7
4	8	5	6	7	3	5	8	2	3	3	8

Four-way Experiment:

Fm	Fd	Bs	Yp
2	5	6	6
2	5	5	6
3	4	6	6
3	3	3	6
2	4	5	5
3	5	4	6
3	3	6	6
2	4	5	5
3	5	4	6
2	4	3	6